

1941

The inheritance of fleece weights in range sheep

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THE INHERITANCE OF FLEECE WEIGHTS
IN RANGE SHEEP

by

Hans Karl Christian Appel Rasmussen

A Thesis Submitted to the Graduate Faculty
for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject Animal Breeding - Genetics

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I. INTRODUCTION

Wool production is one of the triple functions of sheep from the standpoint of their economic value in animal husbandry. In certain areas of the world wool still constitutes the most important source of revenue from sheep flocks whereas in other areas meat and milk production assume a more important role. However, in nearly all cases wool continues to be an important source of revenue from a flock of sheep.

In the range areas of North America wool and meat are the two commercially important products whereas milk production is indirectly important insofar as it affects the early life of lambs dependent on this source of nutrients for their livelihood. A general estimate among range sheepmen is that wool constitutes about 40 per cent of the revenue from the flocks while meat contributes about 60 per cent of the total revenue. These proportions fluctuate from time to time with the relative sales value per unit of the two products. Another factor that influences these proportions is the relative amount of each item produced per breeding unit in the flock. Increase in either product without decrease in the other would change the proportionate value of each while improvement in both

would lead to increase in total revenue from a given number of sheep.

Increase in the value of wool from each sheep or from a flock may result from an improvement of the environmental conditions under which the wool is produced. It may also be achieved through an improvement in the hereditary productive ability of the sheep. Improvement of the hereditary productivity can best be directed on the basis of a thorough understanding of the problems involved.

In recent years a considerable number of investigations have been made into the inheritance of certain fleece characteristics but relatively little attention has been given to fleece weight. Yet, in general, this is the characteristic that bulks largest in the view of the practical sheep breeder as far as wool is concerned. His interest in wool grades, i.e., fiber fineness, crimp, and character, is secondary to his interest in the amount of wool produced. Therefore it seems important to study the problem of the inheritance of fleece weights in order to clarify our knowledge regarding this characteristic and possibly provide for a more intelligent approach toward its improvement. The present study has been made with this purpose in view.

The earliest studies on inheritance were made before the underlying biological laws were known. The studies were based

on a statistical analysis of the resemblance between parent and offspring. With the coming of Mendelism interest naturally swung to breeding experiments to determine the biology of inheritance. Interest in the statistical approach was sidetracked for a number of years.

Despite the tremendous progress that has been made in the science of genetics during the present century its direct application to the improvement of domestic farm animals has been limited. This is because of the complexity of their genetic formulae and the limitations imposed on direct experimentation on these animals because of the high cost of maintaining them for this purpose in sufficient numbers. This is further accentuated by their relatively low reproductive rates.

In recent years it has become more and more evident that a return to the statistical methods was necessary for the study of the inheritance of the genetically complex economic characteristics in farm animals. This could be done logically on the background of fundamental genetic laws provided through the direct experimental attack on plants and laboratory animals.

Fortunately the groundwork for the statistical attack has been laid in the form of mathematical techniques of analysis that provide the tools for studying the heritability (i.e., the relative importance of heredity and environment in causing vari-

ability) of economic characteristics. Not only have the theoretical aspects of this method been probed but sufficient data of various kinds have been analysed to indicate that satisfactory estimates of heritability can be obtained in this way. This then will be the method used in the present study.

II. REVIEW OF LITERATURE

A review of literature showed that few investigations have been directed at the study of inheritance of fleece weights. A considerable number of crossing experiments have been conducted with widely divergent breeds, as well as with some more closely related in terms of wool production. In practically all of these the data on fleece weights have been collected in the course of experiments conducted primarily for other purposes. Data obtained from these experiments indicate a hereditary basis for fleece weights but they are not directly applicable to the present study and will not be included in this review of literature.

The earliest approach to a study of the heritability of fleece weights took the form of investigating the relative influence of individuality (i.e., genotype and permanent environmental effects) and environment on successive fleeces produced by the same sheep. Hill (1921) found a correlation of $.51 \pm .09$ between the weight of fleeces produced by individuals in a group of 30 wethers on the range and the weights of fleeces produced by the same sheep kept for three years in a feed lot. He found that the correlation between the weight of fleeces produced the first year in the feed lot and the last two years

in the feed lot was $.70 \pm .07$. The regression coefficients were .45 and .76, respectively. Hill concluded that: "The variation in the amount of wool produced by sheep in typical range flocks is great enough and sufficiently influenced by heredity to make it certain that culling is a good means of increasing the average weight of fleeces in a flock without a radical change in the type of sheep." The qualification with which the statement ended presumably indicated the author's belief that body type and characteristics especially essential to range sheep were not inimical to increase in wool yield.

Lush and Jones (1923) obtained an average correlation of .607 between the fleece weights from the same sheep in successive years in a large band of Rambouillet ewes in Texas. The authors stated: "Culling will increase the average weight of fleeces for the flock of sheep which is culled and it will also increase the wool producing qualities of the next generation in so far as the individual differences in the sheep culled are hereditary. There are reasons for thinking that very much of this individuality is inherited."

Gärtner and von Ungern-Sternberg (1938), in a study of the biometric relations of various characteristics in sheep, found a correlation of $.61 \pm .04$ between yearling fleece weight and life wool yields.

Terrill (1939) reported a correlation of .59 between the yearling fleece weights and the lifetime average (2 to 5 years) fleece weight for 323 Rambouillets.

Vaughan, Joseph and Vinke (1927) and Joseph (1928) did not agree with other workers on the importance of the repeatability of fleece weights in relation to the improvement to be expected in selection for fleece weight. Joseph (1928) presented data from several groups of Rambouillet ewes. In one group of 234 ewes he found the correlation between first and second fleece weight to be $.29 \pm .04$, between second and third $.69 \pm .02$, and between third and fourth $.82 \pm .01$. In another group of 69 ewes the correlations were: between first and second fleece $.71 \pm .04$, between first and third $.63 \pm .05$, and between second and third $.84 \pm .03$. Other correlations, for some of the same sheep grouped in a different manner, were slightly lower but none were below $.51 \pm .04$. In all except one case the author found a higher correlation between consecutive fleeces than between fleeces separated by two or more years. In this respect his data were comparable to those of Lush and Jones (1923). However, he differed with them in the significance that he attached to these correlations as he emphasized the small improvement that could be obtained by culling unless the culling was very rigorous.

Johansson and Berg (1939) analyzed data from the records of four breeds of sheep in Sweden. The average intra-herd correlation (which they used as their measure of repeatability) was about .35 and ranged from .33 for 210 Cheviot sheep to .37 in the Swedish Landrace in which 112 sheep were studied. Data from 289 Oxfords yielded a correlation of .35 and 304 Shropshires gave a correlation of .36. The authors considered that differences between sheep were to a large extent genetic as the differences between full sisters were distinctly less than those between half sisters. On the basis of their data, Johansson and Berg estimated that not more than one-third of the variance in fleece weights of single fleeces was determined genetically.

Thomson (1925), who worked with data from several mutton breeds in Alberta, obtained an average correlation of .72 between fleeces from individual sheep. Some of his groups were small but for a group of 95 grade ewes the correlation between first and second fleece was .61. In a smaller group of 69 ewes the correlation between second and third fleece was .55 and in a third group of 26 ewes the correlation between third and fourth fleece was .44. Some of the smaller groups gave higher correlations as would be indicated by the higher average. Data for several years were pooled in calculating the correlations for the various groups, i.e., they were not on an intra-year

basis, so this and possibly other factors would tend to cause the correlations to be unduly high.

Phillips et al (1940) have reported on the daughter-dam correlations and regressions of unscoured fleece weights for 649 pairs of Corriedales and 638 pairs of Rambouillets. The correlations were calculated on an intra-year, intra-sire basis for the progeny but the authors did not make clear whether year differences were eliminated from the dams of a group of daughters born in a single year. For fleece weights all the correlations were positive for both breeds though there were large differences in the numerical values of the coefficients from year to year. The authors did not record the mean correlations for the data from each breed but an estimate of these was obtained by the writer of this thesis through the use of the z transformation (Fisher, 1938) for averaging correlations. The range of the correlation coefficients was from .03 to .51 for the Corriedales and from .01 to .40 for the Rambouillets. The corresponding mean values were .30 and .17. The mean values of the regression coefficients were .30 and .19 respectively when each regression coefficient was weighted relative to the number of degrees of freedom associated with it. The authors pointed out that, because of the correlation between daughter and dam, the heredity of the dams would have some influence on the variation of the daughters, though this would be rather

small because of the low correlations.

The only other published data on the correlation between dam and daughter fleece weight appear to be those given by Briggs (1938). He obtained a correlation of .58 for a small group of Rambouillet sheep but his data were limited and should be considered as preliminary data only.

III. SOURCE OF DATA

The data utilized in this study were obtained from two sources. Data for the Canadian Corriedales and the Rambouillets were from the records of the flock at the Dominion Experimental Station, Lethbridge, Alberta. Those for the Romney crossbreds were from the Dominion Range Experiment Station, Manyberries, Alberta. The data for the Canadian Corriedales were from sheep born in the period 1930 to 1939, for the Rambouillets 1933 to 1939, and for the Romney crossbreds 1936 to 1939, inclusive.

To provide the proper background a short review of the breeding history of the various flocks appears to be desirable. The Canadian Corriedales, so named to distinguish them from New Zealand Corriedales, originated in 1919 through the cross of a Lincoln ram on selected Rambouillet ewes. Female progeny from this cross were mated to New Zealand Corriedale rams and this grading was continued, with selection, until 1934. By that time it had become evident that the New Zealand type of Corriedale was not the type best suited to the range conditions of Western Canada. Therefore, it was decided to interbreed the graded Canadian Corriedales and to select for a type with more open faces and a finer grade of wool than that typical of the New Zealand Corriedales.

This interbreeding was based on establishing inbred lines, with different degrees of inbreeding, accompanied by selection. This plan has been followed but because of the relatively slow reproductive rate of sheep, the length of generations, and the fact that many of the non-inbred ewes are still in the flock, the average degree of inbreeding has not risen very high in the intervening time. Therefore, it is believed that the inbreeding has had little, if any, effect on the fleece weights during the time in which the data have been collected. It may have had some effect on increasing the average genotypic resemblance between sheep within lines.

The Rambouillet data for the first few years were obtained from a small flock of pure bred Rambouillets maintained at the Station for a number of years. The breeding system used was typical of that employed in most small flocks with rams being introduced from outside sources at regular intervals. In 1938 the flock was augmented by the purchase of 125 yearling ewes and 75 mature ewes from four breeders in Montana and Utah. Only the yearlings (obtained from three different breeders) and their progeny were included in this study. Considerable care was exercised in selecting these ewes for uniformity of length of staple and density of fleece. Still there is evidence from the two-shear fleece weights (produced while all the sheep were under similar conditions at the Station) to

show that there were real differences in the wool producing ability of the groups obtained from different sources.

The Romney crossbreds at the Dominion Range Station originated through a cross of twelve Romney rams, purchased from a breeder in Oregon, on selected grade Rambouillet ewes in 1935. The F_1 progeny from this cross were interbred, without close inbreeding, to produce the F_2 generation. Only F_1 and F_2 data were available for this study.

The general care and management of the sheep has differed between Stations but at each location the conditions have been relatively constant except for environmental factors over which control could not be exercised. The sheep at the Lethbridge Station have been on range in the mountains during the summer months except in 1935 and 1936 when they were on prairie range. During the fall and winter months they have been kept at the Station which is located in an irrigated area. In open weather pasture has been provided by grain and alfalfa stubble. When the weather prevented winter grazing and during the breeding season, when the sheep were in the breeding pens, alfalfa hay and some grain was fed. Lambing started about the first of April each year and usually extended over a period of about five weeks. Shearing has taken place usually in the second week of May at which time the average age of shearlings would be about thirteen months.

At the Range Station the sheep have been maintained under range conditions such as exist in the drier, short-grass plains area of Western Canada. Very little winter feeding has been done except for the ewe lambs. These have at times been wintered on stubble fields and given supplemental feed. An effort has been made to keep the replacement ewe lambs in good growing condition and to keep all sheep vigorous and thrifty. Lambing at the Range Station usually started about the first of May and continued for about five weeks. Shearing was done usually the first week in June.

At the Lethbridge Station shearing was done by machine until 1933. Since that time blades have been used. At the Range Station blades were used until 1940 but in that year a change was made to machine shearing. These changes would have an effect on the weight of shearling fleeces but because of the method of handling the data, to be explained later, this factor should not be important. The fleece weights were taken immediately after the fleeces were removed from the sheep and had been rolled and tied for packing. The weights were taken to the nearest tenth of a pound as recorded on milk scales of good quality. No skirting or sorting was done but heavy dung locks were removed if they were present.

Shearing was done only when the fleeces were in proper condition and never when they contained an excess of moisture.

Furthermore, all the yearlings were usually sheared in one or two days so changes in weather conditions during shearing time would have little effect in causing variability of fleece weights. If this precaution had not been taken wet weather or strong, drying winds could easily have had a considerable effect on the weight of fleeces from day to day.

Only shearing fleeces (i.e. fleeces shorn when the sheep were approximately one year old) have been utilized in this study of heritability as more data were available in this age class than in any other. The Canadian Corriedales provided data from 206 pairs of dams and daughters, the Rambouillets 70 pairs, and the Romney crossbreds 213 pairs for this study.

IV. AGE CORRECTION

As the lambing season each year extended over a period of about five weeks it appeared that differences in age at the time of first shearing would require some consideration. Joseph (1928) hinted at this when he divided certain of his groups into March ewes and May ewes. Likewise, it was considered by Spencer et al (1928). These workers used a simple proportional factor based on the assumption of a linear rate of wool production throughout the year. Thus the average shearling fleece weight divided by the average age of all shearlings at shearing time yielded an estimate of the production of wool per day. Such a factor is direct and simple but the question arises whether it provides the most accurate measure under all conditions.

An age correction factor that would reduce the known sources of non-genetic variation in fleece weights would be very desirable. Therefore, this problem was investigated with the data available. The data available for this purpose were from a greater number of individuals than were available for the remainder of this study as all shearling ewe fleeces were utilized regardless of whether the ewe later became a dam.

Age per se would be only one of the items included in an

age correction factor if lambs born during one period of the lambing season were affected by certain environmental conditions to a greater extent than lambs born at another period of the season. Several such conditions are believed to have existed in the flocks from which these data were drawn. Conditions may vary from flock to flock but somewhat similar relationships may be expected to occur in most large flocks.

First, there is the observation that lambs born during the first few days of the lambing season are not usually as strong and vigorous as those born later in the season. The exact causes of this are not known definitely though it appears that some of the lambs are slightly premature. Under strictly range conditions the ewes that lamb first would not have had the benefit of better weather and new grass to the same extent as those that lamb later. Likewise, because of the grass situation, the later lambs usually get a better supply of milk as soon as they start nursing. Factors of this kind would tend to reduce any age advantage that the very early lambs might otherwise have.

At the other end of the lambing season there are three factors that tend to accentuate the age difference by affecting more adversely the younger lambs than those born earlier. This is especially true of the lambs born at the Lethbridge Station. There lambing usually starts about the first of April.

Shearing is done during the second week in May. At shearing time the lambs are separated from their mothers during the day for two or three days, though with them at nights. This separation would have a more deleterious effect on the younger lambs than on the older ones. In extreme cases it might lead to a ewe becoming lost from her lamb.

Shortly after shearing time the sheep are dipped. This does not cause separation of ewes and lambs except for a very limited time but the handling attending the dipping affects the sheep unfavorably. This again would be more serious for the younger lambs than for the older ones.

Finally, shortly after dipping, the sheep are trailed about one hundred miles to summer range in the mountains and once more the older lambs fare relatively better than the younger ones. Thus there are three known factors that may affect the lambs. In each case the effect would be of a growth retarding nature, affecting younger lambs more seriously than the older ones. These effects would increase age differences over and above that they would be if all lambs had equally favorable conditions throughout their first year of life. Therefore, it appears that a simple proportional correction factor may not be very accurate, at least under conditions such as apply to the flocks being studied.

The problem then becomes one of correcting in a way that will give due consideration to all of the known environmental

factors that varied with date of birth. These factors would vary in their relative effect from year to year. The proportion of total lambs born in any one week during the lambing season would also vary from year to year. Therefore, it seems evident that a separate correction factor would have to be calculated for each year. This would require a large number of individuals each year and these were not available in the present data.

In order to show the data bearing on this subject the shearling fleece weights for the Canadian Corriedales have been tabulated, by week of birth of the sheep, for a number of years. These data are shown in Table 1.

These data show that there is little uniformity of decrease in fleece weights with decreasing age in the various years. When the means of all years are considered a fairly uniform decrease is indicated though the small number of items in the later weeks cause fluctuations inherent to small samples.

It may be argued that as 94 per cent of the lambs were born during the first three weeks, age correction cannot be very important. Nevertheless, the individuals at the late extreme require the greatest correction, and if not corrected, are the cause of some non-genetic variation that should be controlled. The effect that a proper correction would have on the correlation cannot be estimated but would depend on

the relative effect it had on the covariance and the separate variances of daughters and dams.

Because of the limited data in any one year it was not possible to obtain an adequate correction factor for these data so it was decided to use the data without correction.

Table 1

Table of the Canadian Corriedale shearling ewe mean fleece weights by
week of birth of the sheep

	1st week		2nd week		3rd week		4th week		5th week		6th week	
Year	Num-	Mean	Num-	Mean	Num-	Mean	Num-	Mean	Num-	Mean	Num-	Mean
of birth:	ber	fleece	ber	fleece	ber	fleece	ber	fleece	ber	fleece	ber	fleece
		wt. lb.:		wt. lb.:		wt. lb.:		wt. lb.:		wt. lb.:		wt. lb.
1930	4	9.05	9	9.49	2	8.24						
1931	8	8.84	5	8.40	6	8.42	1	9.10				
1932	8	10.96	9	8.49	7	9.97	1	8.80	1	8.60		
1933	6	10.68	9	9.64	11	10.44	2	10.55	1	9.20		
1934	7	10.27	17	9.56	9	9.41						
1935	9	8.10	13	8.52	18	8.28					2	6.40
1936	12	7.88	18	7.90	10	7.36	1	7.50	2	6.45	2	6.20
1937	7	9.88	13	9.85	3	8.10			3	7.20		
1938	12	7.48	26	7.77	12	7.12			1	6.20	1	6.60
1939	15	8.29	13	8.21	12	8.15	3	7.93			1	6.00
Total	88		132		90		8		8		6	
Weighted mean		8.88		8.66		8.52		8.79		7.31		6.30
Un-weighted												
mean		9.14		8.78		8.55		8.78		7.53		6.30

V. ANALYSIS OF DATA

A. General Considerations

Correlations, regressions, and analysis of variance were the statistical tools employed in analyzing the available data. These procedures are quite standardized and require no general discussion in this paper. Their application will be discussed with each phase of the analysis.

It is generally agreed that the phenotypic expression of a quantitative characteristic is conditioned by both the genotype and the environment. Therefore, in analyzing the present data it was necessary to consider the influence of certain environmental factors known to affect fleece weight. These factors may be classified into two main categories, namely, those that apply in common to all the sheep and those that have their effect limited to individual sheep within the flock. The latter class may include things that affect only certain individuals and not others; it may consist of differential responses to certain environmental factors by various individuals; or both effects may be combined. Environmental factors that have a permanent effect on an animal, and thus would constitute part of the individuality of that animal, would fall into this group.

The permanent environmental effects plus the effect of the genotype would determine the permanent differences that would exist, and could be measured, between animals. On the other hand environmental effects, peculiar to certain animals, could also give rise to temporary differences between animals but these effects could not be segregated and would be included in unanalyzed causes of variation.

The environmental factors may be sub-divided further into two classes, namely, those that influence wool growth and those that affect fleece weight after the wool has been grown. The first class would comprise all the factors that influence the physiological state of the sheep and thus affect the rate of wool growth. Factors in this group could have either temporary or permanent effects.

One of the most important of the factors affecting wool growth is the general plane of nutrition during the first year of a sheep's life, when pregnancy and lactation do not occur. The plane of nutrition would be common to all except in the early life of the animals when they are dependent mainly on the milk supply of their mothers. This factor may be relatively important for, while it may be overcome partially in later life, it is reasonable to suppose that at the shearling age it may be the cause of some of the differences between individuals.

The second class of environmental factors, i.e. those that affect the fleece weights after the wool has been grown, would be mainly common to all sheep within a flock and would have no permanent effects. The weather, i.e. the prevalence of rain and wind, ranks first among this second class of factors, as it determines, to a large extent, the cleanliness of the fleece. For example, in a dry, windy year, such as occurs quite frequently in Southern Alberta, the fleeces of the sheep at the Lethbridge Station would contain a higher proportion of soil matter than in a wet year or a year in which relatively heavy snowfall occurred and persisted during the winter. At the Manyberries Range Station this would not be so important as dust storms are not prevalent because of the greater distance from farming areas.

To anyone familiar with wool it is evident that the effect of this second group of environmental factor could be eliminated almost completely if the data could be analysed on a clean wool basis. This has not been possible for the data included in this study. Furthermore in the practical selection of sheep, unscoured fleece weights must be used. Consequently an approach to the problem of the inheritance of fleece weights on the basis of unscoured fleece weights appears to be logical.

Fortunately, it has been shown that in unselected groups of fleeces there is a fairly high correlation between unscoured

fleece weight and yield of clean wool. Spencer et al (1928) found the correlation to be $.62 \pm .01$ for 990 Rambouillet fleeces. Malan et al (1935) reported the correlation to be .67, .80, .79 for three separate years. Terrill (1940) obtained a correlation of .69 for 186 yearling fleeces from Rambouillet sheep. Thus it is evident that unscoured weight constitutes a fairly reliable measure of the wool producing ability of sheep though the use of unscoured weight rather than scoured weight retains a source of error in the data.

The problem in analysing the data then becomes one of cancelling out the effects of common environment, eliminating year to year differences, and dealing, as far as possible, with only those factors that cause differences between individuals within each year. Different methods of accomplishing this have been used for the various analyses and these will be discussed in the particular sections of this paper to which they are applicable.

B. General Statistics of the Populations Used in This Study

Before progressing into a detailed analysis of the main subject of this thesis it is desirable to present a general summary of the means and standard deviations of the shearling

fleece weights produced by the three flocks under study.

Such a summary is presented in Table 2.

The compilation in Table 2 includes all shearling ewe fleeces produced by the respective groups during the years under consideration. The differences between mean fleece weights and standard deviations within breed groups are significant. Factors causing the differences in means are quite evident but factors leading to differences in variability within years are more obscure. Year to year differences in shrinkage, i.e. the amount of material other than wool in the fleece, (in this case especially soil matter) were very great and alone could account for the differences in means though other factors also could be involved. The factor of annual differences in shrinkage would not be so important in affecting variability within years. It is quite possible that differences in fleece types would lead to variation in amount of soil content under similar conditions of exposure and this might account in part for the differences in variability. Thus in years when no dust storms occurred all the fleeces would be relatively clean and variability from this source would be low. In years when dust storms were prevalent some fleeces would permit entry of a relatively greater amount of soil than others and this would lead to increased variability.

Table 2. Statistics of shearing fleece weights for the three breed groups

Year	Canadian Corriedale		Rambouillet		Hornsey crossbred		Mean	C. V. %	n	Fleece	wt.	Birth
	Mean	C. V. %	Mean	C. V. %	Mean	C. V. %						
1930	16	9.00	1.07	11.9								
1931	20	8.62	.98	11.4								
1932	26	9.66	2.09	21.6								
1933	29	10.21	1.25	12.2	7	8.67	1.60	18.4				
1934	33	9.67	1.19	12.3	6	9.20	1.21	13.2				
1935	42	8.23	1.24	15.1	8	7.70	1.73	22.5				
1936	45	7.62	1.10	14.4	3	6.70	1.15	17.2	192	6.28		
1937	26	9.35	1.79	19.1	11	9.13	.73	8.0	202	7.58		
1938	52	7.51	1.14	15.2	52	7.98	1.31	16.4	67	8.79		
1939	44	8.15	1.01	12.4	43	7.43	1.12	15.1	146	6.87		
Totals												
Averages												
	332	8.60	1.30	16.1	130	7.94	1.25	15.7	607	7.13		
											1.10	15.4

Note: Throughout this paper the year designates year of birth but fleece weight data are for the following season.

The Canadian Corriedales produced the heaviest fleeces as shearlings though the Romney crossbreds are not strictly comparable with the other two groups as they were raised under different conditions. The difference between the Corriedales and the Rambouilletts constitutes a real breed difference.

Standard deviations calculated on an intra-year basis for the pooled data for each group differ slightly. The coefficient of variation (C.V.), which expresses variability relative to the mean fleece weights, shows that on this basis the variability within each breed group is practically the same.

The estimate of the standard deviations of shearling fleece weights in these data are lower than those obtained by Phillips et al (1940) for somewhat similar data. However, their mean fleece weights were higher and when coefficients of variation were calculated for their data it was found that these were slightly lower (13.7, 14.6, and 14.6 for Columbias, Corriedales, and Rambouilletts respectively) than those obtained for the present data.

C. Repeatability of Fleece Weights

As indicated in the review of literature, there have been several studies of the repeatability of fleece weights from individual sheep. It was deemed advisable to determine the repeatability of fleece weights from individual sheep in the flocks used in this study as this would provide a new data ^{added} on the subject. More important still it would help show whether these flocks were comparable to others that have been studied. Should they be similar in this respect, the general applicability of the findings in the remainder of this paper would be indicated and more confidence could be placed in them from that standpoint.

The procedure used in this section of the paper was an analysis of variance with a subsequent calculation of the intra-class correlation. The intra-class correlation can be used as a criterion of repeatability of fleece weights because it measures the degree of resemblance between the weights of several fleeces from the same sheep. That is, it measures the variance between pairs of fleeces picked at random for the same sheep as compared to the variance between pairs of fleeces picked at random from all the sheep. If the variance between fleece weights of different sheep is greater than the variance between fleeces from the same sheep it indicates that there must be permanent differences between sheep, provided that they are all

maintained in the same general environment. These permanent differences are caused by hereditary factors and by the permanent effect of environmental factors peculiar to each animal.

All sheep that produced three fleeces in their first three years of life were included in this analysis. This provided a maximum of data and the results may be considered to be applicable to later years as well. The sheep used in this analysis were, in a general way, the same as those used for other phases of this thesis study though not entirely the same individuals throughout. There were 196 Corriedales, 81 Rambouillets, and 282 Romney crossbreds, each with three consecutive records.

The analyses were made separately for each of several years. They were then combined to provide a pooled estimate of the intra-year, intra-class correlation for each breed. A summary of the results is given in Table 3.

In the analysis of variance it was found that the differences between sheep were highly significant which also means that the intra-class correlations were highly significant. Furthermore their numerical value is great enough for them to be of practical importance. They show that one fleece weight provides a useful estimate of the weights of succeeding fleeces, relative to the mean of fleece weights in the population. For example, if sheep were selected because they

had a fleece weight one pound above the average of the population of that year they could be expected to have fleece weights the following year that would average at least one-half pound above the mean fleece weight of the same population in that year.

Table 3

Intra-year, intra-class correlations (used as a measure of repeatability) by years and as a pooled estimate for each of the three breed groups

Year of birth	:Canadian Corriedales:			:Rambouillets			:Romney crossbreds		
	:Number	:Intra-class	:Number	:Intra-	:Number	:Intra-	:Number	:Intra-	
	:in	:correlation:	:in	:class	:in	:class	:in	:class	
	:group	:	:group	:correla-	:group	:correla-	:group	:correla-	
	:	:	:	:tion	:	:tion	:	:tion	
1930	11	.24							
1931	15	.35							
1932	22	.44							
1933	29	.53	6	.31					
1934	26	.57							
1935	29	.54	15	.72					
1936	39	.63	40	.52	166	.41			
1937	25	.79	20	.63	116	.46			
Total									
Number	196		81		282				
Average									
intra-year,									
intra-class									
correlation		.56		.56		.43			

Another way of showing the relative importance of the various sources of variance was to break down the variance into its component parts by the method outlined by Fisher (p.228, 1938). The results are shown in Table 4.

Table 4

Analysis of variance, in actual units of variance, of three consecutive fleeces from ewes of the three breed groups

Source of variation	Units of variance		
	Canadian Corriedales	Rambouillets	Romney Crossbreds
Between years	3.96	6.42	2.11
Between sheep	1.28	.94	.66
Between fleeces from the same sheep	1.01	.75	.87

This analysis indicates that the variance between fleeces from the same sheep was largest in the Corriedales, intermediate in the Romney crossbreds, and smallest in the Rambouillets. The permanent differences between sheep were in the order: Corriedales, Rambouillets, Romney crossbred. The analyses further showed that the ratio of the variance between fleeces to the variance between sheep was of a different order in the Romney crossbreds than in the other two groups.

The variance between years was of considerable magnitude in all cases. A large part of this was introduced by age differences within groups. One of the three fleeces included for each sheep was the shearling fleece and the other two were the second and third shear fleeces. The difference between the means of the shearling fleece weights and the means of the other two fleeces was about 3.0 pounds so this would cause much of the variation noted between years. Other factors of an environmental nature would also contribute to this variation.

The permanent differences between sheep include the additive gene effects, the dominance deviations, and the epistatic effects, as well as permanent effects of environmental factors affecting individuals in unlike manner. The additive effects are the average effects that are produced in that population by substituting a gene for its allele. They would be the actual effects if such a substitution in any gene complex always resulted in the same plus (or minus) change in the phenotype regardless of what other genes were present. It is known that many genes do not behave in this manner but have a greater or less effect depending on what other genes are present. Such discrepancies between the average effect of that gene substitution and its actual effect in particular genotypes constitute deviations due to dominance or to epistatic interactions.

Dominance refers to non-additive relations between allelic genes. If any degree of dominance exists the substitution of the more dominant gene into a homozygous recessive produces a larger phenotypic effect than the substitution of the same gene for the remaining recessive one in the heterozygote.

Epistatic effects are caused by interactions of various kinds between non-allelic genes in a gene complex. Therefore, the effect of a gene substitution depends on whether its interacting non-alleles are present or absent.

The relative importance of each of these three kinds of gene effects may vary from characteristic to characteristic. The separation of the dominance and epistatic effects from the additive effects usually is difficult and often impossible in quantitative characters. However, it has been shown that even in cases where extreme epistatic and dominance conditions are known to exist a large part of the actual genetic variance can be expressed in terms of additively genetic variance. Where epistasis and dominance are not extreme the most of the hereditary variance will be included in the additive portion. (Lush 1937).

In these data it may be noted that the estimates of repeatability are of the same order as those obtained by the authors mentioned in the review of literature. Thus in a

general way the data being studied may be accepted as representative of those obtained from range sheep. There is the question of whether the repeatability coefficient for the Romney crossbreds is actually different from the repeatability coefficients of the other two groups or whether the difference is due to sampling error. This was tested by the method outlined for intraclass correlations by Fisher (1938). It was found that the difference between the Corriedales and the Romney crossbreds was significant at the five per cent level. The difference between the Rambouillets and the Romney crossbreds was not significant. The lack of significance in this latter case, despite the similarity of the correlations for the Corriedales and Rambouillets, was caused by the smaller number of animals in the Rambouillet group yielding a larger estimate of variance. Analyses presented later in this paper further indicate that there may be a real difference in hereditary variance between the Romney crossbreds and the other two groups.

D. Daughter-dam Correlations and Regressions

One method of obtaining an estimate of the heritability of a characteristic is through studying the likeness between parent and offspring. In the present study this was limited to the resemblance between dams and daughters as the male offspring, kept to shearling age, were too limited in number

to provide adequate data. A study of the likeness between sires and daughters would not have provided as much information as the daughter-dam likeness because the sires were much fewer in number and had been subjected to more rigorous selection.

Both correlation and regression were used to measure the parent-offspring resemblance. The latter offered some distinct advantages in overcoming possible errors caused by selection of the dams. In order to obtain the most accurate estimate of these statistics it was necessary to eliminate, as far as possible, the environmental factors that might affect them. This matter has already been discussed and only the details of how this was accomplished need be mentioned here.

In calculating the daughter-dam correlation and the regression of daughter fleece weight on the fleece weight of the dam the adjustment for environmental influences was accomplished by grouping the pairs of daughters and dams on a double intra-year basis. That is, all daughters born in one year were placed in sub-groups with dams all born in a single year. Thus the sheep in each daughter sub-group would have been subject to the same general environmental influences applying to the flock that year and each sub-group of dams would all have been under similar general environmental influences. Differences between contemporary individuals then would be caused by genetic dif-

ferences and by the environmental factors peculiar to each individual. Environmental factors common to animals in each sub-group of dams and in each sub-group of daughters would cancel out.

Grouping on this basis led to the formation of 31 sub-groups for the Canadian Corriedales, 13 sub-groups for the Rambouillets, and three sub-groups for the Romney crossbreds. The variance and the covariance was calculated separately for each sub-group. These were then pooled to provide an estimate of the average correlation and regression coefficients for each breed by the method outlined by Snedecor (1938). The coefficients thus obtained were on an intra-year basis; i.e. concerned deviations from the average of contemporaries in the same flock. The summarized data for the Canadian Corriedales are presented in Table 5.

Some of the sub-groups are very small and little, if any, significance can be attached to the differences in the correlation coefficients. A correlation coefficient based on two items necessarily must be either +1. or -1. and therefore is almost meaningless by itself. Nevertheless, when the variances and covariances are pooled each such small group adds one more degree of freedom and is of some value in increasing the accuracy of the estimate of the average correlation coefficient.

Table 5

Analysis of covariance of Canadian Corriedale shearling
ewe fleece weights

No.	: Number of:	: Group: daughter:	: Sx ²	: Sxy	: Sy ²	: r	: Year of:	: Average
No.	: dam pairs:	: in group:	: (Dam):	: (Daugh-:	: ter)	: r	: birth	: r's
No.	: in group:	: (Dam):	: (Daugh-:	: ter)	: r	: r's	: by years	: ters
1	4	1.47	5.50	27.67	.86	1932	.862	
2	5	6.26	4.28	7.23	.63	1933	.688	
3	3	4.83	2.40	1.28	.96			
4	5	14.43	2.29	6.65	.23	1934	.441	
5	6	4.04	3.14	6.95	.59			
6	10	8.24	7.54	18.72	.61			
7	6	5.73	-1.40	13.93	-.16	1935	.247	
8	11	3.95	-1.47	14.39	-.20			
9	11	59.07	14.66	12.10	.55			
10	5	4.87	2.64	6.03	.49			
11	2	0.61	0.38	0.25	1.00	1936	.016	
12	6	3.94	-1.58	3.21	-.44			
13	8	19.47	0.93	7.66	.76			
14	10	16.06	-1.49	10.34	-.12			
15	12	6.28	2.41	11.97	.28			
16	3	0.61	-0.81	1.09	-.99	1937	.154	
17	5	8.38	1.29	4.43	.21			
18	8	7.15	1.63	8.58	.21			
19	2	0.18	-0.33	0.61	-1.00			
20	5	5.33	-1.60	7.75	-.25	1938	.142	
21	6	25.23	-5.64	4.60	-.52			
22	3	3.14	1.56	1.13	.83			
23	4	1.14	0.32	2.33	.20			
24	15	17.02	0.97	15.73	.06			
25	13	13.05	12.39	17.47	.82			
26	2	0.25	-0.56	1.38	-1.00	1939	.190	
27	2	0.72	0.96	1.28	1.00			
28	2	0.61	0.22	0.08	1.00			
29	10	12.68	-1.84	3.28	-.28			
30	13	16.35	-2.89	19.34	-.15			
31	9	26.92	12.59	9.10	.80			
	206	293.01	58.69	246.56	.22			

The correlation coefficient, .22 computed from the pooled data is highly significant when tested with the 174 degrees of freedom available for making the test of significance.

The daughters born in the first three years were by New Zealand Corriedale sires and those in the last five years were by Canadian Corriedale sires. When the data were regrouped so that those for the first three years (first 6 sub-groups) constituted one group and the last five years (last 25 sub-groups) another group the correlation coefficient for the first group was .48 and for the second it was .16. The two coefficients differ considerably but a test of significance of the difference, by means of Fisher's (1938) z transformation, showed that the difference was not significant.

The daughters of the New Zealand Corriedale sires were from flock matings so that the sires for individual daughters could not be identified. Daughters by Canadian Corriedale sires were from pen matings so both the sire and dam were known for each daughter. Therefore, all sections of this paper in which sire effects are discussed will be limited to the 173 daughter-dam pairs in which the daughters were sired by Canadian Corriedale sires. As already mentioned, the correlation coefficient for this group is .16.

Despite the fact that the correlation coefficients were calculated from relatively limited material, it was decided

to investigate the effect of eliminating sire differences from the intra-year variance and covariance of the sub-groups. This was done with the result that the average correlation coefficient was changed very little, merely being reduced from .16 to .14.

The Rambouillet (70 pairs) and the Romney crossbred (213 pairs) data were analysed in a manner similar to that used for the Corriedales. A summary of the results for all three breed groups is presented in Table 6.

Table 6

Average intra-year daughter-dam correlations and regressions for the various groups of sheep				
	Corriedales: Pedigree group	Rambouillet : lets :	Romney :cross- :breds	Corriedales :All :groups
Number of daughter-dam pairs	173	70	213	206
Intra-year correlation	.16	.19	.05	.22
Intra-year, intra-sire correlation	.14	.22	.07	
Intra-year, intra-sire regression	.12	.20	.07	

None of the correlation coefficients are statistically significant so it can not be determined whether the observed differences have any significance. However, the small size of the correlation for the Romney crossbreds would suggest that it may be actually different from the other two.

The elimination of sire effect did not markedly change the numerical values of the correlation coefficients. In the Corriedale group the coefficient was reduced slightly, whereas in the other two groups a slight increase occurred. No significance can be attached to the fact that the changes were not all in the same direction as sampling errors, with small samples, could easily account for the difference.

Some selection for fleece weight was practiced in the flocks being studied though the intensity of selection was not high as numerous other characteristics also had to be considered. While selection may alter the correlation between daughter and dam it does not alter the regression of daughter on dam to any marked degree. This applies when selection is light but if heavy selection were practiced it might decrease the base on which the regression rests and therefore chance fluctuations could be greater than in unselected populations. Because of these considerations it was decided to investigate the regression of daughter fleece weight on dam fleece weight and not to rest the investigation on the correlation alone. The regression provides a direct basis for estimating the possible effectiveness of selection since it is an actual description of how the fleece weights of daughters did increase with each unit increase in the dams.

The regression coefficients were calculated from the pooled estimate of variance and covariance in the usual way. The values

obtained on an intra-year, intra-sire basis are given in the bottom line of Table 6.

To indicate more clearly the form of the distribution on which the correlations and regressions were based the data for the Canadian Corriedales have been plotted in Figure 1. The distribution is that of deviations from each sub-group mean and not actual individual fleece weights. This form was necessary in order to correct for differences in the sub-group means.

As a further check on the data a test for deviation from linear regression was made by the method given by Snedecor (1938). This showed that there was no significant deviation from linearity in any of the three breed groups.

The data in Table 6 show that there was very little difference between the correlation coefficients and the regression coefficients. Because of the relationship between the regression coefficient and the correlation coefficient $b =$

$r_{xy} \frac{\sigma_y}{\sigma_x}$ the small difference between the two in these data indicates that there was little difference in the variation in fleece weights of dams and daughters. This is further indicated in the standard deviations of the dams and daughters of the three breed groups shown in Table 7.

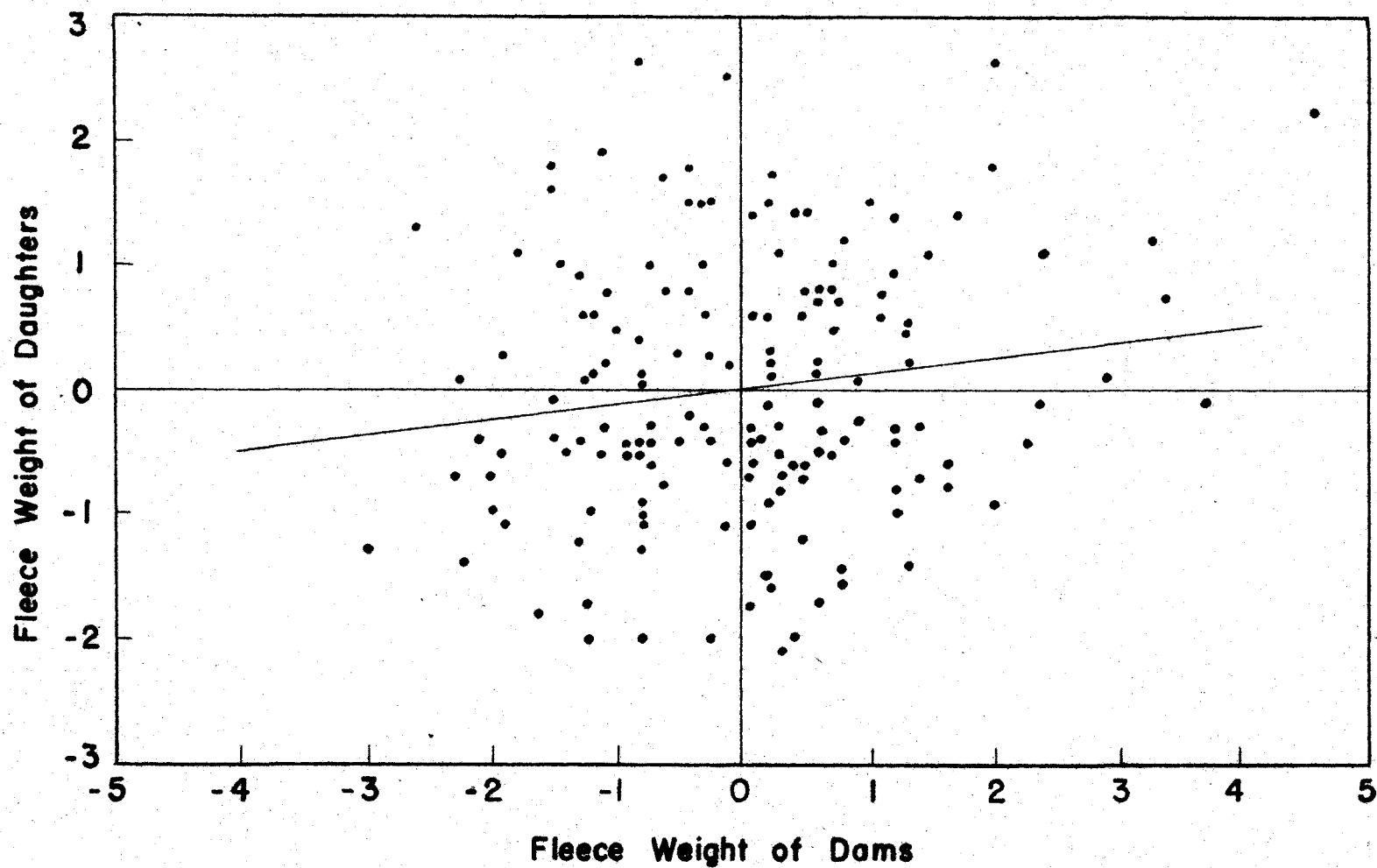


Figure 1. Regression ($b = .12$) of Canadian Corriedale daughter fleece weights on the fleece weights of dams, plotted as deviations from sub-group means.

Table 7

Intra-year, intra-sire standard deviations for
the three breed groups

Breed	σ dams' fleece weights	σ daughters' fleece weights
Canadian Corriedale	1.06	.89
Rambouillet	.98	.87
Romney crossbred	.96	1.05

These data show that in the Corriedales and Rambouillets the variances of the shearling fleece weights of the sheep later chosen as dams were actually larger than the variance of the shearling fleece weights of the daughters. For the Romney crossbreds the variance of the dams was slightly smaller than for the daughters.

These data seem to indicate that the dams did not constitute a selected group though another interpretation is possible, namely, that both the dams and the daughters were selected. Obviously the daughters could not be selected on actual fleece weight before they were sheared at about one year of age. However, indirect selection for fleece weight could be practiced to a limited extent at weaning time. This has been done for the Corriedales and the Rambouillets. At weaning time the ewe lambs were all scored for body and fleece characteristics and animals deficient in staple length and in density were culled out. This was not done with the Romney crossbreds during the years in which the data for the present study were collected.

Spencer et al (1928) found a significant correlation of .24 between density and unscoured fleece weight but a non-significant correlation of -.01 between length of staple and unscoured fleece weight. Malan et al (1935) reported a significant correlation of .34 between fiber length and fleece weight and while fiber length and staple length are not synonymous they are indicative of the same thing. Hill (1921) reported a high correlation of .56 between length of staple and weight of fleece. All these statistics were obtained from data collected at shearing time. Lambert et al (1938) in their studies on the relation of fleece characteristics at weanling and shearling ages found a correlation of .66, .80, and .65 for length of fleece at the two ages for Corriedale, Columbia, and Rambouillet sheep respectively. For density the correlations were .15, .38, and .35 respectively for the three breeds.

Thus while the correlations between fleece weight and length of staple and between fleece weight and density are not high they do indicate that culling the poorest individuals at weaning time would tend to eliminate those with the lightest fleeces. This would lead to a reduction in the variation in the shearling fleece weights of the daughters saved and included in these data.

Some further evidence with regard to the amount of selec-

tion practiced may be obtained from a comparison of the mean fleece weight of the sheep used as dams and the mean for the whole population. It was found that the mean fleece weight of all dams was 9.17 pounds, whereas reference to Table 1 shows that the mean fleece weight of all shearlings was 8.60 pounds. A slight correction should be made to this figure to include only the years from which the dams actually were drawn. This eliminated the 1939 data as these sheep had not yet had the opportunity to become dams. With this group removed the mean fleece weight of the population was 8.67 pounds. Thus the mean of the dams was .50 pounds above the mean of the population from which they were drawn.

E. Paternal Half-sib Correlations

Up to this point consideration has been given to the resemblance between daughter and dam fleece weights. In the present section of the study attention has been given to sire effect and the resemblance between fleece weights of paternal half-sibs. An estimate of these factors has been obtained by analyses of variances and the subsequent partitioning of variance as outlined by Fisher (1938). The data for each breed group were analysed separately in order to bring out differences that might exist between the three groups.

The analysis of the Canadian Corriedale data is shown in Table 8.

The first main point of interest is the relative importance of the various sources of variation, i.e. that caused by differences in years, sires, and individuals within sires. The usual analysis of variance shows that there are significant differences both between sires and between years. However, this does not provide direct information regarding the proportion of the total variation contributed by each cause of variation. In order to determine this a further analysis was made. The results of this analysis are given in the bottom part of Table 8.

In this table the individual variance is the variance caused by differences between pairs of daughters picked at random within the same sire group. These differences are the result of the combined effect of genetic differences between paternal half-sibs and of environmental factors peculiar to each animal.

The variance due to sire differences is a measure of the additional variation caused by differences between sires. That is, individual variance plus variance due to sire differences is the variance that would result from picking pairs from groups of daughters so that the members of each pair would be born in the same year but sired by different sires. Therefore, if differences between sires were present the variance within pairs which had different sires would be great-

Table 8

Analysis of variance of the fleece weights of
Canadian Corriedale shearling ewes

Source of variation	Degrees of freedom	Sum of squares	Mean square
Total	172	295.43	1.72
Between years	4	62.47	15.62**
Within years	168	232.96	1.39
Between sires within years	15	59.23	3.95**
Within sires within years	153	173.73	1.14

Paternal half-sib correlation within years = $\frac{1.39-1.14}{1.39} = .18$

<u>Sources of variance</u>	<u>Portions of variance</u>	
	<u>In actual units</u>	<u>As a percentage of the whole</u>
Year differences	.34	18.9
Sire differences within years	.32	17.8
Individual variance among paternal sibs	1.14	63.3
Total	1.80	100.00

Note: In all analyses of variance in this paper
* indicates significance at the 5% level and
**at the 1% level.

er than the variance within pairs by the same sire.

Variance due to year differences is the additional variance that would result if pairs of daughters were picked in such a way that the members of the pairs would differ in both year and sire.

In view of these considerations it is evident that the individual variance is the base from which the calculations must be made. Then the mean square for sires is the individual variance plus the variance actually contributed by sire differences. Therefore, the individual variance must be deducted from this mean square and the remaining portion must be divided by the average number of daughters per sire to provide an estimate of the variance contributed by each daughter. Likewise the mean square between years is made up of the individual variance, plus the variance caused by differences between annual means. The latter is weighted by the number of daughters per year and must be reduced to a per daughter basis to provide the variance in actual units.

This can be made clearer by providing an example of the actual method of calculation. The Canadian Corriedale data from Table 8 have been used in the following example.

Sources of variance	Mean square	Composition of mean square
Year differences	15.62	$A + k_1B + k_2C$
Sire differences	3.95	$A + k_1B$
Individual variance	1.14	A

A = Individual variance within paternal half-sib groups
 B = Variance added by differences in sires
 C = Variance added by differences in years
 k_1 = Average number of daughters per sire = 8.64
 k_2 = Average number of daughters per year = 33.98

$$A = 1.14$$

$$A + 8.64(B) = 3.95 \quad B = \frac{3.95 - 1.14}{8.64} = .32$$

$$(A + 8.64B) + 33.98C = 15.62$$

$$C = \frac{15.62 - 3.95}{33.98} = .34$$

The total variance is merely a summation of the various parts and in this case would be $1.14 + .32 + .34 = 1.80$.

Ordinarily the procedure is only applicable to data in which the number of individuals in each group (k) is equal. If the groups are of slightly unequal size the use of the average k will not constitute a large source of error but when the groups are very few and very unequal in size, the discrepancy may be important. A correction factor, which compensates largely for this source of error, has been devised by Winsor and Clarke (1940). The correction is that from the

average k is to be subtracted $\frac{V_k}{L}$, where L is the number of individual items and V_k is the variance in group size. This correction will be small if the groups do not vary much in size i.e. if V_k is small. This correction has been used throughout this section in calculating average group sizes for partitioning the variance in these data.

In the present data the total theoretical variance may be defined as the variance that would occur if all pairs were picked in such a manner that members of each pair were born in different years and sired by different sires. In the calculation of the total variance in the usual analysis of variance no such restriction is involved and the pairs are considered as being picked at random from a population made up of individuals born in different years and sired by different sires. In such random pairing some of the pairs would not contain all the causes of variation and therefore the total variance would be lower than in the theoretical case with its restriction on pairs.

In these data the difference between the theoretical total and the actual total is not very great for the Corriedales and the Rambouillets but for the Romney crossbreds it is rather extreme.

By partitioning the variance it was found that, for the Corriedales, 18.9 per cent of the total variance was caused by

differences between years. An almost equal amount, 17.8 per cent, was contributed by differences between sires within years, whereas the greatest portion, 63.3 per cent, was caused by variation between individuals within sire groups. This 63.3 per cent was for sheep born in the same year and sired by the same sire. If it were not for environmental factors affecting individuals in different degree this should constitute the genetic variance caused by differences in dams plus the factor of random sampling of the gene complex of the dam and of the sire. The genetic variance would in this case include the additive, dominance, and epistatic effects and would therefore be greater than the additively hereditary variance. Neither the dominance and epistatic effects nor the environmental factors can be segregated from the strictly additively hereditary portion of the variance by direct methods.

The paternal half-sib correlation as deduced from the reduction in variance when the intra-sire variance was compared with the intra-year variance was .18.

An analysis, similar to that for the Canadian Corriedales, was carried out for the Rambouillets and is set forth in Table 9.

In these data a significant difference was found between years and between sires. The year effect was greater in the Rambouillets than in the Corriedales (31.6 per cent vs. 18.9 per cent). On the other hand the sire effect was somewhat

less (10.4 per cent vs. 17.8 per cent). The differences were opposite but not equal in effect and the result was that individual variance was less in the Rambouillets than in the Corriedales. (58.0 per cent and 63.3 per cent respectively). Likewise the half-sib correlation was slightly lower at .14.

Table 9

Analysis of variance of fleece weights of Rambouillet shearling ewes

Source of variation	Degrees of freedom	Sum of squares	Mean squares
Total	69	123.75	1.79
Between years	4	38.56	9.64**
Within years	65	85.19	1.31
Between sires within years	9	22.73	2.52*
Within sires within years	56	62.46	1.12

Paternal half-sib correlation within years $\frac{1.31-1.12}{1.31} = .14$

Portions of variance

<u>Source of variance</u>	<u>In actual units</u>	<u>As a percentage of the total</u>
Year differences	.61	31.6
Sire differences within years	.20	10.4
Individual variance among paternal sibs	1.12	58.0
Total	1.93	100.0

The analysis of the Romney crossbred data is presented in Table 10.

Table 10

Analysis of variance of fleece weights of Romney crossbred shearling ewes

Source of variation	Degrees of freedom	Sum of squares	Mean squares
Total	212	437.18	2.06
Between years	1	168.89	168.89**
Within years	211	268.29	1.27
Between sires within years	12	24.83	2.07
Within sires within years	129	243.46	1.22

$$\text{Paternal half-sib correlation within years} = \frac{1.27 - 1.22}{1.27} = .04$$

Source of variance	In actual units	Portions of variance As a percentage of the total
Year differences	1.65	56.2
Sire differences within years	.06	2.0
Individual variance among paternal sibs	<u>1.22</u>	<u>41.8</u>
Total	2.93	100.0

The results in Table 10 require some special attention. The year effect was exceptionally high, constituting 56 per cent of the total variance. On the other hand the sire differences were scarcely significant with the F value at 1.7 whereas for significance at the 5 per cent point it should be 1.8. This lower sire effect is in keeping with the results of analyses made earlier in this paper and indicates that there is relatively less hereditary difference in this group of sires than in the sires of the Corriedale and Rambouillet breeds. A smaller degree of hereditary difference between individuals within sires was also found in the Romney crossbreds.

F. Estimates of Heritability of Fleece Weights

In the preceding sections of this paper the data have been analysed in such a way that certain estimates of resemblance between parent and offspring and between paternal half-sibs have been obtained. The present section will deal with the derivation of estimates of heritability from the statistics previously obtained. This then is merely an extension of the previous analyses to their conclusion.

Wright (1921) has formulated a technique, path coefficients, which provides an efficient method of showing the biometric relationships on which the estimates of heritability are based.

The path coefficient procedure presents in diagrammatic form the assumed and known cause and effect relationships between independent and dependent variables in the various correlations obtained previously.

For clarity of presentation it seems desirable to show the application of this method to one group of data with the necessary path coefficient diagrams and then to provide a summary of the results from all three groups. The Canadian Corriedale data were used for this purpose. In all cases the statistics obtained in the previous analyses have been accepted at face value as the best available estimates of correlation coefficients. New data may show that they are somewhat in error because the samples were small.

The path coefficient diagram, Figure 2, indicates the biometric relationship of the causes that may enter into the daughter-dam correlations.

As the diagram indicates, three major factors may influence the phenotype or production (in this case fleece weight) of the offspring. The sire's genotype and the dam's genotype, plus the chance factor in segregation of their gene complexes, determine the genetic constitution of the offspring. In addition environment plays an important part in determining the phenotypic expression of the offspring and the dam.

The correlation between the phenotype of the dam (P_D) and the phenotype of the offspring (P_O) can be written:

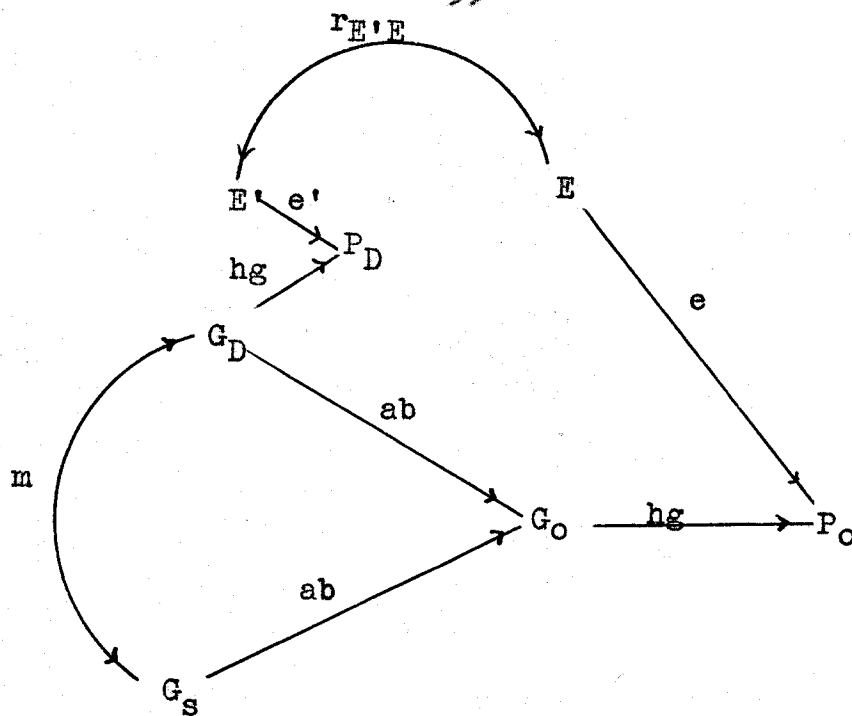


Figure 2. Path coefficient diagram showing cause and effect relationship for daughter-dam correlation of fleece weights.

In this diagram the symbols represent:

G_D = genotype of dam.

G_S = genotype of sire.

G_O = genotype of offspring.

P_D = phenotype of dam.

P_O = phenotype of offspring.

$r_{E'E}$ = correlation between the environment of dam and offspring.

m = correlation between the genotypes of sire and dam.

ab = path coefficient from genotypes of parent to genotype of offspring.

hg = path coefficient from genotype to phenotype.

$$r_{P_D P_O} = abh^2g^2 + abh^2g^2m + e'r_{EE} = .14$$

In the Corriedales the correlation (m) between the genotype of the dam (G_D) and the genotype of the sire (G_S) will have some value greater than zero because of a certain degree of inbreeding in the flock. This inbreeding has been somewhat irregular and has included some sire-daughter matings as well as mainly half-sib matings. On the other hand a considerable proportion of the dams were drawn from a random mated flock and the original matings were to sires from the same flock. In these matings the correlation between genotypes would be practically zero. Therefore, it is estimated that the average value of m would be about .2 for these data.

The correlation (r_{EE}) between the environment of the dam and the daughter may be assumed to be zero in these data. This assumption rests on the fact that in a relatively large flock, such as the one from which these data were drawn, special attention cannot be given to individual sheep with respect to feed and general care. Consequently the environment to which all dams and all daughters were subjected would be uniform in the sense that it would have no special tendency to be above average for both members of a daughter-dam pair or below average for both.

Then for a solution of the equation above:

$$ab = \frac{1}{2}$$

$$m = .2$$

$$r_{E'E} = 0$$

$$\text{whence } \frac{1}{2}(h^2g^2 + .2(h^2g^2)) = .14$$

$$1.2 h^2g^2 = .28 \text{ and } h^2g^2 = .23$$

This would be the maximum estimate of the additively hereditary portion of the variance. If $r_{E'E}$ had any positive value, h^2g^2 , the additively hereditary variance, is overestimated.

Proceeding in a similar manner it is possible to obtain an estimate of h^2g^2 from the paternal half-sib correlation. The diagram for the relationship of independent and dependent variables is shown in Figure 3.

In this case the equation is:

$$r_{P_0P_0} = a^2b^2h^2g^2 + 3 m a^2b^2h^2g^2 + e^2 = .18$$

$$a^2b^2 = \frac{1}{4} \quad m = .2 \text{ as before.} \quad e^2 = 0$$

$$\text{Then } \frac{h^2g^2}{4} + \frac{.6 h^2g^2}{4} = .18 \quad \text{and } h^2g^2 = .45$$

The assumption that e^2 is zero is logical in this case because the various groups of contemporary paternal half-sibs were raised under the same environmental conditions. All were in the same flock and the various groups were all mixed together as soon as they were born. The situation here is quite different from that existing if data from several flocks had been combined. Under the latter conditions differences in the

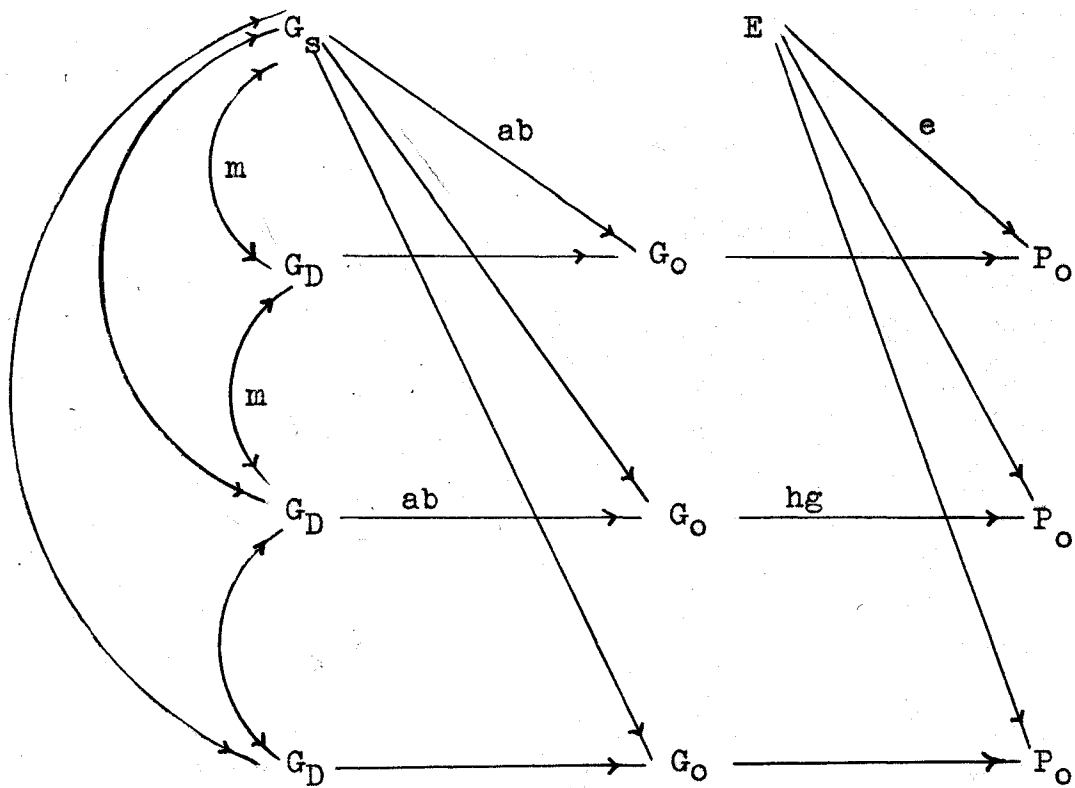


Figure 3. Path coefficient diagram of the cause and effect relationship for the paternal half-sib correlation.

In this diagram the symbols are the same as those used in Figure 2.

treatment of the various flocks could lead to an environmental correlation.

An additional estimate of the additively hereditary variance may be obtained by a simple doubling of the regression of daughter on dam. This was done and in Table 11, in which the various estimates have been summarized, it may be noted that this estimate is practically the same as the estimate derived from the daughter-dam correlation coefficient.

Using the procedures, just discussed, estimates of heritability were obtained for both the Rambouillets and the Romney crossbreds. These have been included in Table 11.

In these data the range of the estimates of the additively hereditary variance is large both between breed groups and within breed groups. Within breed groups the estimate from the paternal half-sib correlation differs more from the other estimates within the Corriedale group than is the case for the other two groups. In this connection it should be emphasized that any error or bias in the half-sib correlation is multiplied by four. Consequently it may be less reliable than the estimates obtained from the daughter-dam correlations and regressions.

Table 11

Summary of estimates of the additively
hereditary variance (h^2g^2) for the three
breed groups

Source of estimate	Corrie- dales	Rambouil- lets	Romney cross- breds
	h^2g^2	h^2g^2	h^2g^2
From daughter-dam regression	.24	.40	.14
From daughter-dam correlation			
$r_{E'E} = 0$ $m = 0$.28	.44	.14
$r_{E'E} = 0$ $m = .2$.23	.37	.12
From paternal half-sib correlation			
$E = 0$ $m = 0$.72	.56	.16
$E = 0$ $m = .2$.45	.35	.10

VI. DISCUSSION

The analyses made in this paper have provided estimates of the resemblance between fleeces from the same individuals, between fleeces of daughters and dams, and between fleeces of paternal half-sibs. All the analyses have been based on a study of the variance in the different breed groups and each separate analysis has served to segregate and compare certain fractions of the variance and the covariance.

The repeatability of unscoured fleece weights was found to be .56, .55, and .43 respectively for the Corriedales, Rambouillets, and Romney crossbreds. These were all intra-year estimates. In numerical value they are quite similar to estimates of repeatability obtained by previous workers. For example, Lush and Jones (1923) obtained an average repeatability of .607 for somewhat similar data. Their estimate as well as those obtained in the present study were based on unscoured fleece weights. The estimates would include the repeatability of grease and suint production as well as wool production. Nothing definite is known of the repeatability of these additional characteristics but it may be expected that it would be about the same as that of wool.

Environmental factors affecting the fleece weight after the wool was grown would cancel out to a great extent. The exception would be where certain environmental factors affected one type of fleece more than another. For example, a relatively long stapled but loose fleece might contain more foreign matter, such as soil, than a short, dense stapled fleece would. The degree of difference would vary from year to year depending on climatic and range conditions. Such environmental factors would tend to reduce the repeatability of unscoured fleece weights as compared to scoured fleece weights.

Apparently they are not highly important except under special conditions. Lush and Jones (1923) obtained an average repeatability coefficient of .607 for Rambouillet sheep under range conditions. On the other hand Johansson and Berg (1939) obtained estimates ranging only from .33 to .37. Their data were on mutton type sheep under farm conditions in Sweden and it may be that the environmental factors there would be of the kind that would lower the repeatability. Another factor was that the breeds they studied were not primarily wool sheep such as those from which all the other data have been obtained. This suggestion is somewhat weakened by the fact that Thomson (1925) obtained coefficients of repeatability higher than any others reported though his data were from mutton type sheep managed under farm conditions.

In view of the evidence from the various sources it seems safe to conclude that the repeatability of fleece weights of range sheep will average about .5 or slightly over.

For the Corriedales, Rambouillets, and Romney crossbreds the intra-year, intra-sire daughter-dam correlations were .14, .22 and .07 respectively. Whether the differences between these correlations are real could not be determined from the present data. However, the fact that all the analyses indicated less hereditary variability in the Romney crossbreds than in the other two groups would tend to justify the belief that the correlation for this group is lower than would normally be expected among range sheep. This idea is supported by the data provided by Phillips et al (1940). These authors obtained an intra-year correlation of .30 for 649 daughter-dam pairs of Corriedales and .17 for 638 pairs of Rambouillets.

Regression coefficients of daughter fleece weights on the fleece weights of dams had practically the same values as the correlation coefficients. In this study they were .12, .20, and .07 respectively for the Corriedales, Rambouillets, and Romney crossbreds. The coefficients reported by Phillips et al (1940) were .30 for Corriedales and .19 for Rambouillets.

While the regression coefficients are not high they do indicate that selection may be useful in increasing the fleece weights in succeeding generations. However, for every increase

of a pound in dams' fleece weights the maximum increase in daughters' fleece weights would be .20 pound if the regression coefficients from the present data are accepted as valid estimates. This assumes that the sire was equal in breeding ability to the average of the group of dams from which the dams were selected. The use of a sire selected to equal the breeding ability of the selected dams would lead to a doubling of the progress indicated above. The most serious obstacle to this type of progress is that selection of dams to average one pound above the population mean is not easily attainable as long as other characteristics have to be considered. It can more nearly be achieved with the sires as the number required is considerably lower than the number of dams required.

The paternal half-sib correlations differ to almost the same extent as the daughter-dam correlations. However, in this case the Corriedales were highest with .18, the Rambouillets in the middle with .14, and the Romney crossbreds again at the bottom with .04. The individual variance, in actual units, was practically the same for the Corriedales and Rambouillets. However, the sire difference was considerably greater for the Corriedales.

The differences in sire effect may result from some difference between group of dams being included in sire effect for the Corriedales. The intra-year sire differences provide

a proper estimate of the influence of sires as compared to individual differences, only if no other factors were present that might cause differences between contemporary groups of paternal half-sibs. It can be stated quite definitely that in these data there was nothing in the care and management of the sheep that would lead to such differences. Likewise, in neither the Rambouillet nor Romney crossbred group was the breeding system of such a nature that genetic differences, other than those caused by the sire, would result. With the Corriedales the situation was somewhat different.

As mentioned under "Source of Data," the Canadian Corriedales have been separated into inbred lines in recent years. A considerable number of the original random bred ewes are still in the flock, distributed among the various lines. However, there may have been enough inbreeding to cause greater genetic resemblance between dams within lines than there would be in groups of ewes selected from a random bred population. This would lead to sire differences being accentuated by differences between groups of dams. To the extent that these conditions have occurred the paternal half-sib correlation will be too high for the Canadian Corriedales.

The year differences were highly significant in all three breed groups. This emphasizes the great effect that annual variations in environment play on fleece weights, especially on the weights of unscoured fleeces. Estimates of the shrink-

age of fleeces for the various years indicate that a large part of the year differences would be caused by factors affecting the fleece weight after the wool was grown. The differences also would be caused partly by environmental factors that would affect wool growth but in general these would be less important.

In considering the estimates of heritability it is desirable to keep separate those obtained from the daughter-dam correlations and regressions and those obtained from the half-sib correlations. Reference to Table 11 shows that the estimates range from h^2g^2 values of .14 for the Romney crossbreds when $m = 0$ to .44 for the Rambouillets. If the Romney crossbred data are accepted as being not typical, because of the breeding of this group, the range is narrowed from $h^2g^2 = .24$ for the Corriedales with $m = .0$ to .44 for the Rambouillets. These values may be compared to estimates obtained from the data of Phillips et al (1940) by a doubling of the intra-sire regression coefficients. In these latter data the estimates of h^2g^2 were .60 for the Corriedales and .38 for the Rambouillets. Thus it would appear that the estimates obtained from the data used in this paper are reasonable from the standpoint of not being too high. Whether they represent average values cannot be stated definitely.

The estimates of the additively hereditary variance ob-

tained from the half-sib correlations range from .35 for the Rambouillets to .72 for the Corriedales. One point should be emphasized with regard to these estimates. Any error or bias in the half-sib correlation is multiplied by four in arriving at the estimate of heritability. In the estimate derived from daughter-dam correlations multiplication is by two only and errors would not be magnified to the same extent. It has already been pointed out that the half-sib correlation for the Corriedales is probably too high. Furthermore, the value .72 is based on an m equal to zero whereas its value no doubt is positive. The estimate of h^2g^2 with $m = .2$ was .45 for the Corriedales and this appears to be more nearly the correct value.

This contention is supported by the fact that h^2g^2 cannot be greater than the repeatability. The repeatability coefficient for the Corriedales in these data was .56 which is in line with values from other groups of data. Therefore, this may be taken as a maximum which the additively hereditary variance cannot exceed.

For heritability to equal repeatability, dominance and epistatic effects in determining fleece weights must be zero and there would be no permanent differences caused between contemporary sheep by environmental factors that affected some but not others. It seems unlikely that this could be entirely

true though it may be that dominance and epistasis are relatively unimportant in their effect on fleece weights.

From the analyses presented in this paper it appears safe to conclude that there is sufficient additively hereditary variance in shearing fleece weights to permit selection to be effective in improving fleece weights in the average range flocks of sheep. The greatest difficulty will be that the selection differential, i.e. the degree of selection against low fleece weight, cannot be very high. Part of the reason for this is that numerous other characteristics will also be considered and the greater the number of characteristics considered the less intense will be the selection for any one of them.

Some modification of this last statement may be required if it can be shown that the other characteristics are positively correlated with fleece weight. For example, body weight is a characteristic that receives consideration in the selection of replacement ewes. It has been shown (Gärtner u. von Ungern-Sternberg 1938; Joseph 1931; Brody and Campbell 1938; and Hunt 1935) that there is a fairly high positive correlation between body weight and fleece weight though there was some evidence that this was not entirely linear. That is, under certain conditions the largest ewes were poorer wool producers than medium sized ewes. This is related to the optimum size of ewe for

range conditions where the amount of feed may be such as to limit the productive ability of larger animals.

There is also evidence previously cited that there are positive correlations of varying magnitude between such characteristics as staple length and fleece weight and density and fleece weight. Therefore it may be possible to combine these various characteristics into a compound index such that maximum progress in the improvement of all would be attained. This is a problem to which little attention has yet been given but which is worthy of further study when data can be obtained.

Another factor placing a limitation on the selection differential is the relatively low reproductive rate of sheep and the need for a definite number of replacements. The latter cannot be controlled very much as under range conditions ewes usually must be removed from the flock when they reach the age of five years or six years at the most. The reproductive rate is subject to some control in the matter of rate of multiple births. However, this has practical limits in the economy of sheep production. These limits very likely need revision and should be subject of study especially as related to the effect of twins on selection of replacement stock under range conditions.

The results obtained in this study have been from sheep of one age analysed on an intra-year basis. They may not be the same as would be obtained from a study of sheep of mixed

ages. From the practical standpoint this should have no serious consequences as selection will be practiced mainly within age groups. Shearlings would constitute one age group and mature sheep another group for the purpose of selection. As there is very little difference between the wool production of sheep in the age classes from two to six years these can all be placed in one group without serious error. Most of the selection for fleece weight would be practiced on shearlings and in some cases on weanlings. In the latter case the selection would not be on actual fleece weight but on estimates of differences in fleece weights based on other characteristics.

The data and analyses presented in this paper lend support to the belief expressed by Hill (1921) and Lush and Jones (1923) that an important part of the variability in fleece weights is hereditary and that selection can be useful in improving fleece weights both in the generation in which it is practiced and in the progeny of that generation. Furthermore the estimates of hereditary variance obtained in this study are of the same general order as those of Johansson and Berg (1939) who estimated the hereditary variance to be not over 35 per cent.

VII. SUMMARY

A study of the inheritance of fleece weights of range sheep was made with data from three groups of sheep. These comprised data for Canadian Corriedales and Rambouillets at the Dominion Experimental Station, Lethbridge, Alberta, and for Romney crossbreds at the Dominion Range Experiment Station, Manyberries, Alberta. The first two groups were managed under semi-range conditions and the latter group under strictly range conditions.

Shearling fleece weights were used as this provided a maximum amount of data. Furthermore, from the practical standpoint the main interest in selection and heritability of fleece weights centers on the shearling fleece. Unscoured fleece weights were used as scoured fleece weights were not available. This retained a source of error in the data but again from the standpoint of practical selection unscoured fleece weights usually must be used so it was logical to determine heritability on this basis.

Because the lambing season at both Stations extended over a period of about five weeks each year an effort was made to obtain an age correction factor that would correct for differences in age at the time of first shearing. An analysis of

the available data showed that certain environmental factors had a differential effect on lambs born at different periods in the lambing season. This caused a simple proportionate correction factor of average wool production per day for all shearling sheep to be inadequate. Likewise it necessitated a separate correction factor for each year and the data were not plentiful enough for such a factor to be calculated. Therefore, fleece weights uncorrected for age were used.

In analysing the data consideration was given to environmental factors that would affect fleece weight. These were considered in two categories, namely, those that would affect the rate of wool growth and those that would affect fleece weight after the wool was grown. A further classification distinguished between environmental factors common to all sheep and those peculiar to certain individuals. The former were cancelled out by the methods of analyses employed whereas the latter were included in the differences between individuals.

The data were analysed to show the mean shearling fleece weights, the standard deviation, and the coefficient of variability for the three breed groups. It was found that the mean weights were 8.60 pounds, 7.94 pounds, and 7.13 pounds respectively for Corriedales, Rambouillets, and Romney crossbreds. As the Romney crossbreds were raised under conditions different from the other two groups it was not possible to

determine whether the difference in fleece weights between this group and the other two was caused by hereditary differences, by environmental differences, or by both combined. The difference between the mean fleece weight of the Corriedales and Rambouillets was significant and indicated a real breed difference.

The standard deviations also differed but when the coefficient of variability, which expresses variability relative to the mean fleece weight, was used, the variability within the three groups was practically the same.

In order to test the general resemblance of these flocks to others that have been studied, the repeatability of fleece weights from individual sheep was calculated. For the Corriedales, Rambouillets, and Romney crossbreds the coefficients of repeatability were .56, .55, and .43 respectively. These coefficients were practically of the same order as those obtained by other workers. This indicated that the sheep used in this study were typical of range flocks and the general applicability of the other findings in this thesis was thereby indicated.

Correlations between the fleece weights of daughters and dams were determined on an intra-year, intra-sire basis. They were .14 for Corriedales, .22 for Rambouillets, and .07 for Romney crossbreds. Likewise the regression of daughters' fleece weights on the fleece weights of dams was also determined. They

were .12, .20, and .07 for the three breeds in the same order as above. The regression coefficients provide a description of the increase in daughters' fleece weights that could be expected per unit increase in the fleece weight of dams. Therefore, the regression coefficients indicate that some improvement may be expected through selecting for heavier fleece weights.

Paternal half-sib correlations were obtained as a measure of the resemblance between daughters by the same sire, born in a single year. The correlations were .18, .14, and .04 for Corriedales, Rambouilletts, and Romney crossbreds respectively. The correlation for the Corriedales was higher than for the Rambouilletts, possibly because in this breed inbreeding had caused greater genotypic resemblance between groups of dams than would be true in a random bred population. This would tend to increase the degree of resemblance between paternal half-sibs. It would also tend to accentuate differences between sires disclosed by the analysis of variance.

The analysis of variance further showed that year differences were highly significant for all breed groups. This was caused mainly by environmental differences from year to year but in some cases could also be attributed partly to differences caused through a complete change of sires.

Sire differences were highly significant (1% level) for the Corriedales, significant (5% level) for the Rambouillets, and just below the 5% point of significance for the Romney crossbreds. The low sire effect in the latter group was in keeping with the lower estimates of hereditary variance obtained from the other analyses.

Estimates of heritability were deduced from the correlations and regressions. They ranged from a low of .14 for the additively hereditary variance in the Romney crossbreds to a high of .72 in the Corriedales. This higher estimate was from the half-sib correlation which, as already indicated, was probably higher than would be obtained under random breeding. Furthermore, the estimates from the half-sib correlations were obtained by multiplying these by four, so that any bias or error would be increased to that extent. The additively hereditary variance cannot be higher than repeatability and this would place the maximum at .56 for the Corriedales in the present data.

On the basis of the analyses of the data in this study it seems that the additively hereditary variance is large enough to indicate that improvement in fleece weight can be attained through selection. Because of the limitations placed on selection for fleece weight alone, through the need of selecting for other characteristics, it was suggested that a compound index

should be studied in the hope that this could lead to maximum improvement in several characteristics at the same time.

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IX. ACKNOWLEDGMENT

The author wishes to express his sincere appreciation to all who have assisted in this investigation. To Dr. Jay L. Lush, Iowa State College, special thanks are due for the generous counsel and constructive criticism given throughout the analysis of the data and the preparation of the manuscript. The helpful suggestions and critical reading of the manuscript by Dr. J. W. Gowen, Iowa State College, were very valuable.

Data from the Dominion Range Experiment Station were furnished by Mr. H. J. Hargrave, Superintendent. To Dr. W. H. Fairfield, Superintendent, Dominion Experimental Station, Lethbridge, the author is especially indebted for continual encouragement and advice during the course of this investigation.